Superposition and modulation of muscle synergies for reaching in response to a change in target location

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The control of goal-directed limb movements requires sensory information about the goal and the state of the limb to generate appropriate muscle activation patterns, coordinating the kinematically and dynamically complex multijoint musculoskeletal system and compensating for errors due to noise or perturbations. Because of the latencies in the transmission and processing of sensory signals, preprogramming of the muscle patterns is necessary until sensory information can be used as a feedback signal for error correction. In both cases, knowledge of the kinematic and dynamic characteristics of the musculoskeletal system needs to be exploited for efficient and accurate control. For example, an inverse internal model of the limb geometry and of the musculoskeletal dynamics can be used to map a desired endpoint trajectory into the muscle patterns driving the endpoint along that trajectory (Kawato 1999). A forward model can be used to map an efferent copy of the motor commands into an estimation of the endpoint error to be used in an internal error-correcting feedback loop (Desmurget and Grafton 2000). However, how an internal model might be implemented in the central nervous system (CNS) is still an open question. Any explicit analytical model, even if it could be implemented by a large neural network, it would be impossible to learn efficiently because of the number of degrees-of-freedom and parameters involved (Wolpert and Ghahramani 2000). In contrast, an implicit mapping based on approximating the input-output relationships of the exact model by combinations of a few basis functions might allow for efficient learning and would constitute a modular control architecture.

We have recently provided support to the notion of muscle synergies as basis functions for the generation of the muscle patterns for reaching. We have shown that the muscle patterns for fast reaching in different directions (d’Avella et al. 2006) and for reaching in different directions and with different speeds (d’Avella et al. 2008) are well described by the combination of a few time-varying muscle synergies, coordinated recruitment of groups of muscles with synergy-specific muscle activation waveforms, appropriately scaled in amplitude and shifted in time. Hence, muscle synergies can explain the variations of the muscle patterns for reaching a fixed target, averaged over repeated trials in the same condition. While muscle synergies likely result from a combination of feedforward and feedback signals, they capture the control of unperturbed movements. Averaging the electromyographical (EMG) signals over repeated trials, necessary to unmask structured variations of the motor commands from the fluctuation due to the stochastic nature of EMG signal, also cancels any muscle patterns correcting for the errors due to random variability. Such variability might arise in motor planning, muscle activation, and force generation. Thus it is not clear whether muscle synergies are also involved in generating corrective movements during reaching.

Evidence for feedback-based adjustments of reaching movements dates back to the work of Woodworth (1899). Endpoint accuracy and tangential velocity profiles of fast repetitive aiming movements are affected by vision, suggesting that visual feedback is responsible for corrective responses compensating for inaccurate movement planning or execution. Similarly, accuracy and kinematics of discrete aiming move-
ments without vision of the hand were found to differ from those with vision for movement times of 260 ms or longer (Keele and Posner 1968). While corrections also occur during accurate reaching movements, the mechanisms underlying such corrective responses have been investigated extensively using the “double-step” paradigm, in which a spatial error between the endpoint position and the target position is generated by displacing the target either at a fixed latency from the go signal (Georgopoulos et al. 1981; Megaw 1974; Soechting and Lacquaniti 1983) or during the saccadic eye movement usually occurring shortly after the go signal (Blouin et al. 1995; Desmurget et al. 1999; Goodale et al. 1986; Pelisson et al. 1986; Prablanc and Martin 1992; Sarlegna et al. 2003). In case of fixed latencies $>100$ ms, if the initial and the displaced target locations are in different directions with respect to the start position, the hand is first directed towards the initial target and then the trajectory turns towards the displaced target. For target displacement latencies $<100$ ms, the initial direction of the hand trajectory is intermediate between the direction of the two targets, progressively closer to the second target as the time between the target displacement and the initial movement onset increases (Henis and Flash 1995; van Sonderen et al. 1989). In case of target displacement during the orienting saccade to the first target, because of saccadic suppression, subjects do not perceive the displacement if its amplitude is small with respect to the amplitude of the saccade and the trajectory is smoothly and involuntarily adjusted to terminate on the second target.

Adjustments to reaching trajectories due to target displacement or inaccurate initial movement trajectory may be generated by a continuous modification of the motor commands or by one or more discrete corrective submovements. If the error between the hand and the target is small and no target displacement is detected, as in most cases when the error is due to either an inaccurate trajectory or to a small target displacement during saccadic suppression, an automatic correction mechanism generates smooth trajectory changes that are compatible with continuous online control (Desmurget et al. 1999; Goodale et al. 1986; Pelisson et al. 1986; Prablanc and Martin 1992). In contrast, large target displacements, as soon as they are detected, trigger adjustments to the motor commands that lead to the interruption of the original movement and the substitution with a movement to the new target location (Georgopoulos et al. 1981) or to one or more corrective submovements superimposed to and overlapping with the original one (Burdet and Milner 1998; Flash and Henis 1991; Milner 1992). However, the idea of discontinuous or intermittent control through overlapping corrective submovements has also been put forward to account for the adjustments necessary for fast and accurate reaching towards fixed targets (Carlton 1981; Crossman and Goodeve 1983; Keele and Posner 1968; Meyer et al. 1988).

To date the mechanisms underlying the control of reaching movements in response to a change in target location have been mostly investigated at the kinematic level or by analyzing the changes in muscle activity in a limited number of muscles and movement conditions (Gielen et al. 1984; Megaw 1974; Soechting and Lacquaniti 1983). In this study, we investigate the changes in the activity of many muscles in response to changes in target location during fast-reaching movements in multiple directions in a vertical plane. In particular, we test whether the same muscle synergies used for point-to-point movements are also employed for online corrections and whether the muscle patterns underlying the corrective movements are obtained by the delayed superposition of the muscle patterns for the movement from the first to the second target to the muscle pattern for the unperturbed reach to the first target.

**METHODS**

**Experimental Setup and Protocol**

We investigated the activity patterns in shoulder and arm muscles during fast-reaching movements in the frontal plane to either a target at a fixed location or to a target whose location changed unpredictably after the movement go signal. The experimental apparatus, which is described in detail in our previous report on fast point-to-point reaching movements (d’Avella et al. 2006), consisted of a set of fixed spheres and a handle. A central sphere was used to indicate the start location, and eight peripheral spheres, positioned on a circle at 30 cm from the central sphere on a vertical plane at $\approx 45^\circ$ from each other, were used to indicate target locations. The handle, gripped by the subject, was provided with a reference sphere that had to be displaced from start to target. Start and target spheres (4-cm diameter, made by transparent plastic) could be illuminated from inside by a light-emitting diode and were supported by a structure that allowed to adjust the height of the start sphere to match the height of the elbow of a subject standing with the upper arm along the trunk. Five right-handed subjects (4 males and 1 female, mean age of 29.2 yr, and age range of 23–36 yr) participated in the experiments after giving written informed consent. All experimental protocols conformed to the Declaration of Helsinki, and written informed consent was obtained from all participants according to the procedures of the Ethics Committee of the Santa Lucia Foundation.

Subjects performed blocks of reaching movements while standing with the start and target spheres in the frontal plane at a distance that allowed positioning the reference sphere on the handle close to the start sphere while keeping the upper arm vertical and the forearm horizontal. Within each block, for each one of the eight peripheral targets three different types of trials were performed in random order (Fig. 1): **Radial movements** (Fig. 1A, repeated twice per block) were point-to-point movements starting from the central location towards a peripheral target. **Tangential movements** (Fig. 1B) were also point-to-point movements starting from the peripheral target and reaching one of the two adjacent targets. **Target change movements** (Fig. 1C) were movements from the central location initially toward a peripheral target and, after the go signal, to one of the two adjacent targets. Each trial started, when the reference sphere was positioned at the start location (indicated by an illuminated sphere), with a ready signal (target location illuminated and computer generated tone) followed by a go signal (start location turned off and different computer-generated tone, delay from ready randomly varying from 500 to 1,500 ms) after which subjects were instructed to reach the final target within a given time interval and to remain at the target location for at least 1 s (target hold period). In target change trials, three different delays (50, 150, and 250 ms, fixed within each block) from the go to the target change signals were tested. The maximum time allowed for reaching the target was 550 ms from the go signal for both radial and tangential movements and from the target change signal for target change movements. The time of target acquisition was computed online as the time at which the reference sphere was within 5 cm from the target and its tangential velocity was $<30$ cm/s, and auditory feedback was provided to the subjects if the target was not reached in time. As all unsuccessful trials in each block were repeated, each block had a variable number of total trials and a fixed number of successful trials $[48 = 8$ targets $\times (2$ radial $+ 2$ tangential $+ 2$ target change movements$)]$. Four subjects performed each type of block five times (total 15 blocks), one subject four times (subject 3, total 12 blocks).
Data Collection and Preprocessing

Kinematic and EMG data were recorded continuously during each block. The position and orientation of a marker inserted in the handle gripped by the subjects were recorded using an electromagnetic motion tracking system (Fastrak; Polhemus, Colchester, VT) at 120 Hz. The position of the reference sphere attached to the handle, the actual arm endpoint, was computed using translation and rotation matrices that were determined with a calibration performed with a second marker attached to the handle in place of the reference sphere. EMG activity from up to 16 muscles was recorded using active bipolar surface electrodes (DE 2.1; Delsys, Boston, MA), band-pass filtered (20–450 Hz), and amplified (total gain 1,000; Bagnoli-16; Delsys). In all subjects, EMG activity was recorded from the following muscles: biceps brachii short head, biceps brachii long head, brachialis, pronator teres, brachioradialis, triceps brachii lateral head, triceps brachii long head, deltoid anterior, deltoid middle, deltoid posterior, latissimus dorsi, pectoralis major, trapezius superior, trapezius inferior, and teres major. Infraspinatus activity was recorded in all subjects except subject 1. Correct electrode placement was verified by observing the activation of each muscle during specific movements known to involve it (Kendall et al. 2005). Possible contamination of the EMG recordings by electrical cross-talk from adjacent muscles was assessed by performing a cross-correlation analysis between all pairs of channels. Cross-correlation was computed after notch (50 Hz) and high-pass (10 Hz) filtering the EMG waveforms to remove any possible power line noise and movement artifacts. The peak of the normalized cross-correlation between pairs of EMG waveforms was >0.3 only in five cases (deltoid anterior-deltoid middle for subject 1, teres major-infraspinatus for subject 2, and triceps brachii lateral head-triceps brachii long head, latissimus dorsi-teres major, and teres major-infraspinatus for subject 4). Because of the difficulty in distinguishing cross-talk from synchronous recruitment of motor units in different muscles (Kilner et al. 2002), we did not remove these muscles from the set used for further analyses. However, we verified that the removal of the muscles potentially affected by cross-talk did not change any conclusion drawn from those analyses.

Data acquisition and experiment control were performed on a computer workstation using custom software written in LabView (National Instruments, Austin, TX). EMG data were digitized continuously during each block (1-KHz sampling rate; PCI-6035E; National Instruments). Kinematic data and instruction signals were synchronized with the EMG data by logging the time of each kinematic sample and each signal with a digital counter (100-KHz clock; PCI-6602; National Instruments) started simultaneously with the EMG sampling.

Kinematic and EMG data were then digitally low-pass filtered (15 Hz cut-off for kinematic data, 20 Hz cut-off for EMG data after rectification; finite-impulse response filter with zero-phase distortion) and segmented into individual trials. The EMG activation waveforms were further integrated over 10-ms intervals to reduce the size of the data set.
Data Analysis

Endpoint kinematics. We characterized the movement kinematics of the endpoint (reference sphere) by measuring, for all types of movements, movement onset time, movement end time, and the time of occurrence of the first peak of the tangential velocity. Movement onset and end were identified as the first and last times at which the tangential velocity profile crossed a threshold equal to 10% of its maximum. For target change movements, we also computed the angular deviation of the initial movement direction from the direction of the initial target and the time of occurrence of the peak in the tangential velocity of the estimated corrective movement. The angular deviation of the initial movement direction was computed as the angle between the direction of the endpoint at the first tangential velocity peak and the direction of the target (see Fig. 2, inset). The direction of the endpoint at the first tangential velocity peak was indicated by the vector pointing from the position of the endpoint at movement onset to its position at the time of the first peak of its tangential velocity. The direction of the target was indicated by the vector pointing from the endpoint position at movement onset to the mean position at movement end averaged over all radial movements to the same target. Finally, as target change trajectories can be decomposed as the superposition of a trajectory from the start to the initial target and a delayed trajectory from the initial to the final target (Flash and Henis 1991), we estimated corrective movement trajectories by subtracting from each target change trajectory the mean radial trajectory to the same initial target. The mean radial trajectory was computed by averaging all radial trajectories to the same initial target, after alignment on the time of movement onset and time scaling to equal movement onset to peak speed duration.

Muscle synergy extraction. Muscle synergies were extracted both from point-to-point muscle patterns and from target change muscle patterns. In both cases, muscle activation waveforms were aligned to the time of movement onset, averaged across trials with the same start and target locations and, for target change trials, within one of two bins grouping all trials according to the latency of the peak of the tangential velocity of the corrective movement from the movement onset (bin 1, early corrections, from the 5th to the 50th percentile of the latency distribution; bin 2, late corrections, from the 50th to the 95th percentile). Baseline tonic activity was then subtracted from muscle activity during the movement. Thus phasic averaged muscle activation waveforms were estimated by subtracting a ramp starting at movement onset from the level of average tonic activity from 1,000 to 500 ms before the onset and arriving at movement end to the level of the average tonic activity from 500 to 1,000 ms after movement end, as in (d’Avella et al. 2006). Finally, phasic muscle activation waveforms were normalized in amplitude to the maximum of each muscle across all conditions.

We extracted time-varying muscle synergies from averaged, phasic, normalized muscle patterns for radial and tangential point-to-point movements using a iterative optimization algorithm (d’Avella et al. 2006). The algorithm, initialized to random synergy values, identifies a set of synergies with a given duration (a parameter of the algorithm).

Fig. 2. Examples of kinematics across task conditions. Endpoint trajectories (A) and tangential velocity profiles (B) in the frontal plane of subject 1 for radial movements (n = 30) from the start location (0) to one target (1), tangential movements (n = 30) from the same target (1) to either adjacent targets (2 and 8), and target change movements (n = 10) from the start location to the same initial target (1) and (after a delay of 50, 150, or 250 ms from the go signal) to either adjacent targets (2 and 8). Average endpoint positions at movement onset and end in radial movements are indicated by gray circles (onset: darker gray, end: lighter gray). Position at the time of the first speed peak is indicated by a gray dot. Tangential velocity profiles are aligned to the time of movement onset. A, inset: angular deviation of the initial movement direction (θini) of one target change trial (50 ms), defined as the angle between the vector pointing from the endpoint position at movement onset to the position at the first speed peak (shorter dashed line) and the vector pointing from the average initial position to the average final position in radial movements (longer dashed line).
and the corresponding amplitude scaling and onset delay coefficients that minimize the squared reconstruction error. For each subject, we extracted sets of one to eight synergies with a duration of 500 ms and we selected the number of synergy at which the curve of the reconstruction $R^2$ showed a change in slope, indicating a transition from structured variation explained to unstructured variation due to noise. For comparison, we also extracted time-varying synergies from averaged, phasic, normalized muscle patterns for target change movements. As we hypothesized that the muscle patterns for target change movements were generated by superposition of the same synergies used in point-to-point movements, we used a modified version of the extraction algorithm that allowed for the identification of multiple instances of the same synergy (d’Avella and Bizzi 2005).

Reconstruction of target change muscle patterns by point-to-point synergies and patterns. We tested whether the same set of time-varying muscle synergies capturing the variation in the muscle patterns across movement directions in point-to-point movements, i.e., in either radial or tangential movements, could also reconstruct the muscle patterns for movements to a target whose location changes after the movement instruction signal, involving a voluntary correction, by fitting those point-to-point synergies on the target change patterns. Since the target change patterns involved an initial movement followed by a corrective movement, we allowed for multiple instances of each synergy to be used in the reconstruction. To fit the target change patterns, we used the iterative algorithm modified for identifying multiple synergy instances and we only updated amplitude and timing coefficient through one iteration as for the reconstruction of via-point and reversal movements in d’Avella et al. (2006). We imposed a refractory period of 100 ms to avoid excessive temporal overlap between successive instances of the same synergy.

We also tested whether the target change patterns could be reconstructed by superposition of the entire point-to-point patterns for the corresponding radial and delayed tangential movements. We first aligned the radial movement onset to the onset of the target change movement and the tangential movement peak speed to the peak speed of the corrective movement (estimated by the subtraction procedure described above). We then found, using least mean squares, two scaling coefficients that minimized the pattern reconstruction error.

Comparison of synergy recruitment in point-to-point and target change movements. To compare the recruitment of the synergies extracted from point-to-point movements with their recruitment in target change movements, we used a matching procedure. As each synergy in a target change movement could be recruited more than once or not at all, in each target change movement condition and for each synergy we selected one instance that best matched the recruitment of the same synergy in the corresponding radial condition (i.e., from the same start to the same initial target) and one instance that best matched its recruitment in the corresponding tangential condition (i.e., from the same initial to the same final target). Only synergy instances with an onset within an interval of ±100 ms from the onset of the corresponding point-to-point synergy were considered. For the purpose of this selection, point-to-point synergies and target change synergies matched to radial synergies were aligned on the time of the first speed peak while target change synergies matched to tangential synergies were aligned on the time of the peak speed of the corrective movement. If more than one instance fell within the interval, the instance with the amplitude ($c_i$) and timing ($t_i$) coefficients closest to the corresponding coefficients of the point-to-point synergy ($c$ and $t$), according to the norm $|c_i - c + t_i - t|$, was selected. If no instances were present in the interval, the matched amplitude coefficient was set to zero. If the same instance was matched to both radial and tangential synergies, it was split into two instances with amplitude coefficients ($c_{i rad}$ and $c_{i tang}$) scaled in proportion to the matching point-to-point coefficient ($c_{rad}$ and $c_{tang}$), i.e., $c_{i rad} = \gamma^r c_{rad}$ and $c_{i tang} = \gamma^t c_{tang}$, with $\gamma^r = (c_{rad} + c_{tang})^{-1} c_{tang}$ and $\gamma^t = (c_{rad} + c_{tang})^{-1} c_{rad}$ and matched to the corresponding point-to-point synergies.

RESULTS

Performance and Kinematics

All subjects were able to perform the majority of trials in each condition (Table 1) according to the instructions, i.e., to reach the final target within 550 ms from the go signal (radial and tangential movements) or the target change signal (delayed of either 50, 150, and 250 ms from the go signal). Performance varied across conditions (mean success rate over subjects ranged from 70% for 50 ms target change trials to 94% for tangential trials) and subjects (the mean success rate across conditions ranged from 68% for subject 3 to 97% for subject 5). As unsuccessful trials were repeated within each block, further analyses were performed only on an equal number of successful trials in each condition.

The mean reaction time to the go signal (Table 2) ranged, across conditions and subjects, from 208 ms (subject 2, tangential) to 287 ms (subject 4, target change 50 and 250 ms). Radial and tangential movements showed stereotypical straight paths with bell-shaped tangential velocity profiles (Fig. 2, Table 2).

### Table 2. Reaction time to go signal

<table>
<thead>
<tr>
<th>Subject</th>
<th>Radial (n)</th>
<th>Tangential (n)</th>
<th>Target Change 50 ms (n)</th>
<th>Target Change 150 ms (n)</th>
<th>Target Change 250 ms (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>228 ± 38 (240)</td>
<td>219 ± 39 (240)</td>
<td>209 ± 27 (80)</td>
<td>223 ± 54 (80)</td>
<td>252 ± 62 (80)</td>
</tr>
<tr>
<td>2</td>
<td>224 ± 31 (240)</td>
<td>208 ± 25 (240)</td>
<td>218 ± 25 (80)</td>
<td>235 ± 32 (80)</td>
<td>243 ± 37 (80)</td>
</tr>
<tr>
<td>3</td>
<td>231 ± 49 (192)</td>
<td>236 ± 34 (192)</td>
<td>242 ± 53 (64)</td>
<td>271 ± 48 (64)</td>
<td>285 ± 57 (64)</td>
</tr>
<tr>
<td>4</td>
<td>279 ± 29 (240)</td>
<td>263 ± 28 (240)</td>
<td>287 ± 33 (80)</td>
<td>285 ± 38 (80)</td>
<td>287 ± 36 (80)</td>
</tr>
<tr>
<td>5</td>
<td>234 ± 33 (240)</td>
<td>209 ± 32 (240)</td>
<td>224 ± 27 (80)</td>
<td>236 ± 28 (80)</td>
<td>236 ± 28 (80)</td>
</tr>
</tbody>
</table>

Values are means ± SD of the time interval between go signal and movement onset (in ms) over all successful trials (n) for each subject and condition.
Table 3. *Time of first speed peak relative to go signal*

<table>
<thead>
<tr>
<th>Subject</th>
<th>Radial (n)</th>
<th>Tangential (n)</th>
<th>Target Change 50 ms (n)</th>
<th>Target Change 150 ms (n)</th>
<th>Target Change 250 ms (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>322 ± 39 (240)</td>
<td>306 ± 51 (240)</td>
<td>304 ± 31 (80)</td>
<td>324 ± 52 (80)</td>
<td>346 ± 64 (80)</td>
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<tr>
<td>2</td>
<td>338 ± 32 (240)</td>
<td>322 ± 37 (240)</td>
<td>339 ± 36 (80)</td>
<td>347 ± 32 (80)</td>
<td>356 ± 41 (80)</td>
</tr>
<tr>
<td>3</td>
<td>330 ± 52 (192)</td>
<td>326 ± 35 (192)</td>
<td>342 ± 70 (64)</td>
<td>367 ± 56 (64)</td>
<td>384 ± 54 (64)</td>
</tr>
<tr>
<td>4</td>
<td>367 ± 27 (240)</td>
<td>353 ± 30 (240)</td>
<td>387 ± 37 (80)</td>
<td>378 ± 41 (80)</td>
<td>375 ± 35 (80)</td>
</tr>
<tr>
<td>5</td>
<td>317 ± 46 (240)</td>
<td>284 ± 44 (240)</td>
<td>315 ± 36 (80)</td>
<td>322 ± 33 (80)</td>
<td>320 ± 29 (80)</td>
</tr>
</tbody>
</table>

Values are means ± SD of the time interval between go signal and movement onset (in ms) over all successful trials (n) for each subject and condition.

Table 4. *Time of peak speed of corrective movement relative to target change signal*

<table>
<thead>
<tr>
<th>Subject</th>
<th>Target Change 50 ms (n)</th>
<th>Target Change 150 ms (n)</th>
<th>Target Change 250 ms (n)</th>
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<tr>
<td>1</td>
<td>367 ± 24 (80)</td>
<td>333 ± 38 (80)</td>
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<tr>
<td>2</td>
<td>314 ± 35 (80)</td>
<td>322 ± 43 (80)</td>
<td>315 ± 76 (80)</td>
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<tr>
<td>3</td>
<td>338 ± 32 (64)</td>
<td>331 ± 50 (64)</td>
<td>331 ± 79 (64)</td>
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<tr>
<td>4</td>
<td>377 ± 29 (80)</td>
<td>374 ± 33 (80)</td>
<td>368 ± 46 (80)</td>
</tr>
<tr>
<td>5</td>
<td>316 ± 38 (80)</td>
<td>298 ± 46 (80)</td>
<td>300 ± 53 (80)</td>
</tr>
</tbody>
</table>

Values are means ± SD of the time interval between go signal and movement onset (in ms) over all successful trials (n) for each subject and condition.

In contrast, the kinematic features of target change movements showed variations across trials and with target change delay (Fig. 2, columns 3–5). Most velocity profiles had two distinct peaks, with a delay between the first and the second peak increasing on average with the target change delay. At the shortest target change delay (50 ms), most paths curved towards the final target before reaching the initial target. In this condition, there were differences across subjects with respect to the amount of angular deviation of the initial movement direction from the direction of the initial target. Mean deviation ranged from 6.5° for subject 1 to 30.1° for subject 2. Moreover, a linear regression of the angular deviation as a function of reaction time, significant for all subjects (P < 0.001), indicated that the deviation increased with the reaction time, as previously reported in similar tasks (Henis and Flash 1995; van Sonderen et al. 1989).

The mean time of the first peak in the tangential velocity relative to the go signal (Table 3) ranged from 284 (subject 5, tangential) to 387 ms (subject 4, target change 50 ms). To characterize the timing of the corrective movements observed when the target changed location, we computed the difference between each trajectory, aligned to movement onset, and the average radial trajectory to the same initial target (estimated corrective movement trajectory, see methods). Because of the variability in the initial phase of these corrective trajectories, we used the time of the time of the peak of their tangential velocity to reliably characterize the timing of the corrective movements. The mean peak time of the tangential velocity of the corrective movements with respect to the target change signal (Table 4) ranged from 298 (subject 5, 150 ms) to 377 ms (subject 4, 50 ms). Because these timing distributions had widths comparable to the difference between each pair of adjacent target change delays (100 ms), the distributions of the times of peak tangential velocity of the corrective movement with respect to the movement onset for the three target change conditions overlapped (Fig. 3). Thus, to average kinematics and EMGs across similar conditions, we subdivided all target change trials into two groups (early and late corrections), for each subject, according to the time of peak tangential velocity of the corrective movement, excluding the lowest and highest 5% of the data.

**Muscle Patterns**

We compared the muscle patterns for radial and tangential point-to-point reaching movements with the patterns observed when reaching targets whose locations changed after the go signal. Depending on the initial movement direction, different muscles were responsible for accelerating the arm and thus were active before movement onset. For example, in medially directed radial movements (target 1) anterior deltoid and pectoralis showed an early and strong activation burst and superior trapezius a decrease in postural activity (Fig. 4, columns 1; Fig. 5, blue lines). Not surprisingly, target change muscle patterns with the initial target in the same direction had very similar muscle activation waveforms preceding movement onset (Fig. 4, columns 3–4; Fig. 5, magenta lines). Target change muscle activation waveforms after movement onset were for some muscles close to the sum of the radial waveform and the tangential waveform, delayed by difference between the time of peak tangential velocity of corrective movement and of the tangential movement (Fig. 5, green lines), as for lateral triceps in the medial direction (Fig. 5, row 1). However, for other muscles target change waveforms were significantly different from the superposition of radial and delayed tangential waveforms. For example, when the initial target was in the same medial direction anterior deltoid showed a second peak in the activation waveform not present in either radial or delayed tangential waveforms (Fig. 5, row 2). Thus a visual inspection of the averaged muscle activation waveforms suggested that muscle patterns underlying target change movements were not simply the superposition of muscle patterns underlying the point-to-point movements from the start to the initial target and, after a delay, from the initial target to the final target.

**Point-to-Point Muscle Synergies**

To test whether target change muscle patterns could be obtained by the superposition and modulation of the same time-varying muscle synergies used for point-to-point movements, we first extracted time-varying muscle synergies from averaged, phasic, normalized muscle patterns for radial and tangential movements. For each subject, we extracted sets of one to eight synergies and we selected three synergies as the number at which the R² curve showed a change in slope (Fig. 6A) quantified by the drop of the mean squared error of a linear fit of the portion of the R² curve from N to eight synergies below a fixed threshold of 5 × 10⁻⁴ (Fig. 6B). With three synergies,
the $R^2$ values for the reconstruction of radial and tangential patterns ranged from 0.84 (subject 1) to 0.75 (subject 5). The duration of the synergies was chosen as 500 ms by visual inspection to ensure that muscle bursts could be fully captured by each synergy. However, synergy duration was not a sensitive parameter of the synergy extraction algorithm as the $R^2$ of the reconstruction with three synergies as a function of synergy duration showed a plateau for durations >200 ms (Fig. 6C). As shown previously (d’Avella et al. 2008, 2006), each synergy comprised both synchronous and asynchronous synergy-specific muscle activation waveforms of different groups of muscles spanning different joints (Fig. 7A) and each synergy was modulated in amplitude with a characteristic cosine directional tuning (Fig. 7B) and was recruited with specific onset times in the directions where is was most active (Fig. 7C). We used a colored rectangular surface to illustrate the combined directional modulation of amplitude and timing coefficients (Fig. 7D).

The synergies extracted from point-to-point muscle patterns were similar across subjects (Fig. 8, A and B). Similarity between pairs of synergies was computed as the maximum of their normalized scalar product over all possible time-shifts, as in d’Avella et al. (2006). The 15 synergies extracted from point-to-point muscle patterns in all five subjects could be grouped according to their similarity (Fig. 8B) into three groups (Fig. 8A, columns 1–3), indicating that the most distinctive features of the three synergies were shared across subjects. The mean similarity across all pairs in each group was $0.85 \pm 0.03$ (SD) for W1, $0.77 \pm 0.07$ for W2, and $0.70 \pm 0.06$ for W3. For each subject, the three point-to-point synergies were also similar to the synergies extracted from target change patterns (Fig. 8, C and D). The mean similarity across all subjects was $0.88 \pm 0.04$ (SD) for W1, $0.86 \pm 0.05$ for W2, and $0.91 \pm 0.04$ for W3. Thus the structure of the time-varying synergies did not depend on the extraction condition.

Across subjects, synergy W1 (Fig. 7, A and B, red; Fig. 8A, column 1) typically showed an initial burst in trapezius (both superior and inferior regions), anterior deltoid, pectoralis, followed by a strong burst in both heads biceps brachii, brachialis, and brachioradialis (elbow flexors) and in pronator teres and lateral triceps and was maximally active for upward and medially directed movements. Synergy W2 (Fig. 7, A and B, green; Fig. 8A, column 2) showed a temporally complex pattern of synergy-specific muscle activation waveforms characterized by an initial burst in latissimus dorsi, teres major, both heads of triceps brachii together with a reduction in the postural activity (negative phasic waveforms) of biceps brachii, trapezius superior, and anterior deltoid, followed by a burst in biceps brachii and anterior deltoid. This second synergy was maximally active for downward movements. Synergy W3 (Fig. 7, A and B, blue; Fig. 8A, column 3) was maximally active for lateral movements and showed a strong burst in medial and posterior deltoid, trapezius, and infraspinatus (Fig. 8A). Such muscle synergy organization and directional tuning matched closely those previously reported for the phasic muscle patterns of radial movements in the frontal plane (d’Avella et al. 2008).

**Reconstruction of Target Change Muscle Patterns by Point-To-Point Synergies**

We then used, for each subject, the set of three synergies extracted from radial and tangential movements to reconstruct all averaged, phasic muscle patterns for target change movements. We allowed multiple instances of each synergy to be recruited when fitting the target change patterns (see METHODS). The $R^2$ values of the reconstruction of target change patterns ranged from 0.67 (subject 3) to 0.78 (subject 5), indicating that three point-to-point synergies captured most of the data variation also for the target change patterns. Figure 9, columns 1–4, illustrates some examples of the reconstruction of target change patterns by superposition and modulation of point-to-point synergies. The muscle pattern for medially directed radial
movements (Fig. 9, column 1, 0→1) was reconstructed by the activation of all three synergies, with W₂ amplitude (indicated by the height of the rectangles below the EMG traces with the mean muscle waveform in green) larger than W₁ and W₃ amplitudes. The activation waveform of pectoralis (see also Figs. 4 and 5) was underestimated by the synergy reconstruction but the shape of the reconstructed waveform (thick black line) matched well the observed waveform (thin line and gray area, correlation coefficient 0.99) suggesting a deviation from linearity for this muscle. The pattern for the tangential movement from the medial to the medial-lower target (Fig. 9, column 2, 1→2) was also reconstructed by the activation of all three synergies but with a larger amplitude and earlier onset for W₃ and a smaller amplitude and later onset for W₁ than in the radial movement to the medial target. The target change muscle patterns for changes from the medial target to the medial-lower target for both early and late corrections (Fig. 9, columns 3–4, 0→1→2) were also well reconstructed by the synergies extracted from radial and tangential movements. In terms of synergies, some features were captured by a superposition of the same synergies recruited as in the corresponding radial and delayed tangential movements. However, capturing other features required a change in amplitude or timing of synergy recruitment. For example, the first recruitment of W₂, in both early and late corrections, occurred with amplitude and timing similar to those of the radial movement. In particular, the peak of the mean synergy activation waveform (green area in the rectangle below the EMG traces) was near the first peak of the endpoint tangential velocity (second dashed vertical line) in the radial movement and in both target change movements. In contrast, the recruitment of W₁ observed in the radial movement was not present in the early target change pattern and the recruitment of W₃ in the late target change case had a lower amplitude and a later onset than expected from a simple superposition of the radial and tangential recruitment of that synergy. The remaining muscle patterns of Fig. 9, columns
coefficients of the three synergies in radial movements (Fig. 10, row 1, reproducing Fig. 7D), of the instances of the same synergies in clockwise target change movements (row 2: early; row 3: late) matching the radial synergies, of the synergies in tangential clockwise movements (row 4), and of the synergy instances in clockwise target change movements (row 5: early; row 6: late) matching the tangential synergies. All three synergies appear to be recruited with similar directional tuning of amplitude and timing coefficients in point-to-point and corresponding target change movements. However, the amplitude coefficients of the target change synergy instances appear to be reduced with respect to the point to point movements, especially for tangential synergies. We then quantified the changes in the amplitude coefficients across movement types in all subjects by averaging them over different movement directions (Fig. 11). Movement type (point-to-point, target change early and target change late) did not have a significant effect (P > 0.05, one-way ANOVA) on the synergy amplitude coefficients for radial synergies and matched instances in all cases (3 synergies × 5 subjects) but significant effect (P < 0.01) on the synergy amplitude coefficients of tangential synergies and matched instances in 7 out of 15 cases (subjects 3 and 5: W2 and W3; subject 4: all 3 synergies; in addition, P = 0.028 for W1 of subject 3). Thus the target change muscle patterns were reconstructed by the superposition of the same time-varying muscle synergies recruited in the corresponding radial and tangential movements, but the synergies were recruited in three of five subjects with smaller amplitude coefficients in the tangential (corrective) component of the target change movements.

Reconstruction of Target Change Muscle Patterns by Point-To-Point Pattern Superposition

Finally, we compared the error of the reconstruction of target change muscle patterns by point-to-point synergies with the error of the reconstruction by superposition of the corresponding radial and delayed tangential patterns (Fig. 12). The tangential patterns were delayed by the difference between the peak of the tangential velocity of target change correction and of the tangential movement (see methods). To take into account differences in the peak tangential velocity between the different movements and associated amplitude differences in the muscle patterns, both radial and tangential patterns were scaled in amplitude by two coefficients minimizing the error in the reconstruction of the target change movements. The $R^2$ values were much lower for the reconstruction by point-to-point pattern superposition, with a decrease ranging from 0.10 (subject 4, late) to 0.40 (subject 2, early). In contrast, the $R^2$ values for the reconstruction of radial and tangential patterns by the synergies extracted from those patterns were higher than those for the reconstruction of the target change patterns by the same synergies by amounts ranging only from 0.04 (subject 4, early) to 0.12 (subject 2, late). Thus the muscle patterns underlying the corrective movements necessary to reach a target whose location changes after the movement instruction signals were better described by the modulation and sequencing of the same set of time-varying muscles synergies involved in point-to-point synergies than by the superposition of the entire point-to-point muscle patterns.
DISCUSSION

Basic Findings

Fast-reaching movements to a target whose location changes after the go signal require online adjustments to the motor commands based on visual information. Our results indicate that the muscle activity patterns underlying those adjustments are largely generated by the same mechanisms responsible for the muscle patterns involved in reaching to a fixed target. We were able to capture most of the variation in the muscle patterns, recorded from up to 16 shoulder and elbow muscles during fast-reaching movements from a central location towards initially one of eight different targets arranged on a circle in the frontal plane and to one of the two adjacent targets, with either an early or a late corrective movement, by the superposition of multiple instances of three time-varying muscle synergies extracted from the muscle patterns recorded during point-to-point radial and tangential movements between the same targets. Moreover, while at the kinematic level there is evidence for superposition of the endpoint trajectory from the start location to the initial target with the trajectory, appropriately delayed, from the initial to the final target (Flash and Henis 1991), at the muscle level we found that the muscle patterns underlying target change movements were not accurately captured by the delayed superposition of the corresponding point-to-point patterns, even after amplitude modulation. To fit the target change patterns, it was necessary to modulate in amplitude and timing the recruitment of the point-to-point time-varying muscle synergies employed in the corresponding radial and tangential point-to-point movements.

Online Trajectory Corrections by Synergy Superposition and Modulation

We have previously shown that the muscle patterns for fast reaching to a fixed target in different directions (d’Avella et al. 2006) as well as in different directions and with different speeds (d’Avella et al. 2008) are well described by the combination of a few time-varying muscle synergies, coordinated recruitment of groups of muscles with specific activation waveforms (d’Avella et al. 2003; Klein Breteler et al. 2007). Time-varying muscle synergies may thus represent a set of basic modules for the generation of the muscle patterns required to perform all conditions of a task by selection of a small number of parameters, i.e., one recruitment amplitude and one onset parameter for each synergy instance. However, the muscle patterns for reaching to a fixed target, especially if high accuracy at final position is not required, can be largely preprogrammed and do not provide much information on the mechanisms underlying corrective actions. Moreover, because muscle synergies are extracted from muscle patterns averaged over repetitions of the same movement condition, any adjustment in the muscle patterns for reaching to a fixed target generated to correct for random errors in motor planning, muscle activation, and force generation is likely canceled out by the averaging and thus the resulting synergies mainly capture the organization of the motor commands used in unperturbed reaching control. The present results on the organization of the muscle patterns in response to a change in target location indicate that time-varying muscle synergies are also involved in the adjustments of the muscle patterns driven by

Fig. 6. Selection of number and duration of synergies extracted from radial and tangential muscle patterns. A: for each subject (different gray levels), sets of one to eight time-varying muscle synergies were extracted. In all subjects, three synergies were selected as the number at which the curve of the fraction of total variation explained by the synergy combinations ($R^2$) as a function of the number of synergies showed a change in slope (arrow), indicating that four or more synergies would explain only a small additional fraction. B: change in slope was determined by computing the mean SE (MSE) of the fit of a line from N to $N_{\text{max}}$ (8) to the $R^2$ curves of each subject and using a threshold of $5 \times 10^{-4}$ (horizontal dashed line). C: duration of the synergies (500 ms, corresponding to 50 data samples) was chosen to ensure that muscle activity bursts, indentified by visual inspection, could be fully captured by each synergy. However, reconstruction $R^2$ with 3 synergies as a function of synergy duration showed a plateau for durations $>200$ ms, indicating a low sensitivity for this parameter.

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visual information, suggesting that unperturbed control and online corrections rely on a common modular control architecture. Such corrections may be planned as discrete corrective movements from the initial to the final target locations to be superimposed to the initial movements once the target change has been detected, and they may be implemented by the superposition of a few time-varying muscle synergies after adjusting the synergy recruitment parameters associated to the corresponding corrective point-to-point movement to take into account the different initial state of the musculoskeletal system. Indeed, as the endpoint force generated by muscle activation depends on both the arm posture and on the muscle shortening rate, adjustments in the muscle patterns underlying an isolated point-to-point movement are required to superimpose the same movement as a correction to an ongoing movement. An internal representation of the point-to-point movement corresponding to the desired corrective movement in terms of a few synergy recruitment parameters may simplify the online computation of the necessary adjustments.

The generation of discrete corrective movements during reaching in response to a change in target location (Fishbach et

Irregularities in the velocity profiles of hand movements have been interpreted as due to movement segments, or submovements, by many investigators (Crossman and Goodeve 1983; Keele and Posner 1968; Krebs et al. 1999; Lee et al. 1997; Meyer et al. 1988; Miall et al. 1993a; Milner and Ijaz 1990; Morasso and Mussa Ivaldi 1982; Woodworth 1899). Irregularities in the velocity profiles of hand movements have been interpreted as due to movement segments, or submovements, by many investigators (Crossman and Goodeve 1983; Keele and Posner 1968; Krebs et al. 1999; Lee et al. 1997; Meyer et al. 1988; Miall et al. 1993a; Milner and Ijaz 1990; Morasso and Mussa Ivaldi 1982; Woodworth 1899). In particular, the superposition of two overlapping submovements with minimum-jerk trajectories has been shown to fit well the trajectory of a reaching movement in response to a change in target location (Flash and Henis 1991; Henis and Flash 1995). In contrast, short-latency adjustments occurring even when subjects are not aware of a target displacement have been interpreted as due to an automatic and continuous error correction process (Day and Lyon 2000; Desmurget et al. 1999; Goodale et al. 1986; Gritsenko et al. 2009; Pelisson et al. 1986; Prablanc and Martin 1992) distinct from voluntary and intermittent generation of corrective submovements. However, disentangling the contribution of discrete corrective movements from continuous adjustments on the basis of behavioral observations and kinematic measurements may be impossible because both mechanisms can generate similar short-latency smooth adjustments to the reaching trajectory. Similarly, it might be difficult to determine the conditions in which each putative mechanism is engaged, such as size of the error and whether it is processed by the nervous system as a performance error or as a change in the environment (Wei and Kording 2009). In contrast, our finding that a common spatiotemporal organization of the muscle patterns, captured by a small set of time-varying muscle synergies, underlies both point-to-point and the trajectory adjustments in response to a large target displacement supports the idea of a flexible yet intermittent error correction mechanism. The release of discrete corrections, through the recruitment and modulation of muscle synergies, may be the result of a threshold-based decision process relying on continuous accumulation of afferent and efferent information to generate an estimate of final endpoint-target error.

**Design of the Study and Limitations of the Interpretation**

The design of the experiment and the choice of unperturbed movement directions and target displacements were based on the experimental design and apparatus used in our previous studies of reaching movements (d’Avella et al. 2008, 2006). The goal was to characterize the directional modulation of the
Fig. 9. Example of reconstruction of radial, tangential, and target change muscle patterns by time-varying synergies extracted from radial and tangential data. Group of plots on top (EMGs) shows the observed muscle activation waveforms (thin line and gray area) after normalization to the maximum of each muscle across all conditions and the reconstruction by time-varying synergy combinations (thick line) for subject 1 in two sets of radial, tangential, and target change movements (columns 1–4: radial to target 1, tangential CW; columns 5–8: radial to target 5, tangential CW). $R^2$ of the muscle activation waveforms reconstruction by synergy combination for each movement condition is indicated at the top. Group of plots at middle (synergy coefficients) illustrates the synergy recruitment parameters for each synergy instance (same colors as in Fig. 7) as the height (amplitude) and the horizontal position (timing) of a rectangle with the mean synergy waveform (see Fig. 7). Group of plots at bottom (tangential velocity) shows the corresponding endpoint tangential velocities.
synergy recruitment for both unperturbed and corrective movements and, as a trade-off between directional resolution and maximum acceptable number of trials, we have used eight targets arranged on a circle as targets for the initial center-out radial movements and target displacements to the two targets adjacent to each initial target. In this way the target displacements, corresponding to the tangential movements between adjacent targets, also varied across eight directions for each of the CW and CCW conditions.

There are a number of limitations in the interpretation of the results. First, as time-varying synergies were extracted from muscle patterns averaged over similar trials to unmask the structured variations of the motor commands from random fluctuations due to the stochastic nature of the EMG signal, they capture variability across movement conditions but it is not clear if they can also characterize trial-to-trial or other forms of variability (Kutch et al. 2008; Valero-Cuevas et al. 2009). Second, because the number of target change trials for each movement condition was limited, target change trials were averaged within two bins of the correction latency distribution, irrespective of the actual target change delay, as the distributions of individual delays overlapped (Fig. 3). By averaging trials within a broad range of correction latencies, we might have lost some details of the spatiotemporal structure of the underlying muscle patterns. However, the muscle waveforms for individual trials within each bin were not too differ-

Fig. 10. Directional modulation of synergy recruitment in point-to-point and target change movements. Combined directional tuning of synergy amplitude and timing recruitment coefficients (same format as Fig. 7D) of point-to-point synergies during radial (row 1) and CW tangential (row 4) movements and of synergy instances recruited during target change movements matched (see METHODS) to radial and tangential synergies is shown for subject 1. Point-to-point synergies and target change instances matched to radial synergies are aligned to the time of peak tangential velocity (red vertical lines); target change instances matched to tangential synergies are aligned to the time of the peak of the tangential velocity of the corrective movement (magenta vertical lines).

synergy recruitment for both unperturbed and corrective movements and, as a trade-off between directional resolution and maximum acceptable number of trials, we have used eight targets arranged on a circle as targets for the initial center-out radial movements and target displacements to the two targets adjacent to each initial target. In this way the target displacements, corresponding to the tangential movements between adjacent targets, also varied across eight directions for each of the CW and CCW conditions.

Fig. 11. Modulation of synergy amplitude coefficient in point-to-point and matched target change synergies. For each subject, the amplitude coefficients, averaged across movement conditions, are shown for point-to-point synergies (black bars) and matched synergy instances target change early (dark gray bars) and late (light gray bars) target change movements. Significant post hoc comparisons are shown (*P < 0.05, **P < 0.01, Tukey’s honestly significant difference criterion).
employ a small number of control signals modulated across conditions. However, low dimensionality in the muscle patterns is not necessarily due to the organization of muscle synergies by the CNS and it might derive from the characteristics of the musculoskeletal system and of the limb biomechanics or it might be imposed by task constraints. In other words, the spatiotemporal regularities in the muscle patterns captured by the synergies: 1) might be present in the muscle patterns underlying every arm movement and thus might not be indicative of a specific control strategy; and 2) might be generated by the CNS using a different computational strategy (e.g., optimal feedback control or explicit solution of the inverse kinematic and inverse dynamic problems) and thus the combination of muscle synergies would simply be a parsimonious description of the motor output required for a specific task. The first possibility does not seem very likely as the musculoskeletal system is highly redundant and even the same kinematics can be generated with different muscle patterns. However, such possibility could be ruled out by showing that there are different tasks that require different muscle synergies or even tasks that are not well captured by the combinations of a small number of synergies. For example, one could test whether the muscle synergies observed during reaching are also present when the arm reaches similar spatial locations but with a different goal, such as intercepting a moving target. The second possibility is currently highly debated (Tresch and Jarc 2009). One way of testing whether muscle synergies are simply a parsimonious description of the regularities in the motor output or whether they are actually responsible for generating them is to test the synergy model as a causal model, i.e., to verify a prediction on the effect of an intervention on the mechanism generating the motor output. A noninvasive way of affecting the control mechanism would be using its own plasticity, i.e., the capability of the motor system to acquire new skills and to compensate novel perturbations. This approach is currently being pursued (d’Avella and Pai 2010).

**Hypothetical Neural Substrates**

Unperturbed reaching movements and their online corrections are controlled by neuronal networks widely distributed in cortical and subcortical areas. How muscle synergies and their modulation and superposition may be organized within and across these areas is still an open question. The anatomical organization and the physiological characteristics of the motor cortex make this area a natural candidate for the implementation of the muscle synergies underlying visually guided arm movements. Muscle synergies might arise from the divergent connections of corticospinal neurons onto spinal interneurons and motoneurons, and their spatiotemporal structure might be the result of the activation of specific sequences of neuronal ensembles driven by the dynamics of the recurrent motor cortical network (d’Avella et al. 2008). The parieto-frontal network might instead be involved in the selection and modulation of the synergies to be superimposed for generating online corrections after target displacements, as the role of this area is well established (Pisella et al. 2000). The delayed superposition of two instances of a synergy might occur in response to a change in target location when

![Graph showing R² values for target change reconstruction](http://jn.physiology.org/)

**Fig. 12.** Comparison of the error for the reconstruction of target change patterns by point-to-point synergy modulation and sequencing and by point-to-point pattern superposition. For each subject, the fraction of the total variation ($R^2$) of point-to-point muscle patterns explained by the combination of 3 time-varying muscle synergies extracted from the same data (black bars) is compared with the fraction of variation of the early and late target change muscle patterns explained by the same synergies (darkest and second darkest gray bars respectively) and by the superposition of the point-to-point muscle patterns, appropriately aligned and modulated in amplitude (see text, light gray and white bars).
parieto-frontal inputs to the motor cortex reinitialize the dynamic state of the neuronal ensembles associated to each synergy at the beginning of the sequence. Evidence for some of the physiological mechanisms necessary for a neural implementation of muscle synergy combination and superposition has been obtained recently. With respect to combination, two points in the motor cortex of anesthetized cats generate EMG outputs that sum linearly when stimulated simultaneously (Ether et al. 2006). Concerning superposition, neural activity in motor, premotor, and parietal cortex in monkeys during reaches to visual target and online trajectory corrections (Archambaut et al. 2009, 2011) evolves from the pattern associated with the first movement direction to that associated with the second one and the activity associated with the change of hand path is well predicted from that associated with direct reaches, indicating that online corrections emerge from the same mechanism subtending the point-to-point movements and that the initial and the updated plan of movement can be encoded in parallel within the network.

Conclusions

In sum, the reconstruction of the muscle patterns for fast-reaching movements in response to a change in target location by superposition and modulation of a few time-varying muscle synergies extracted from point-to-point movements suggests that a common mechanism underlies unperturbed control of goal directed limb movement and their visually guided online corrections. These results provide further support to the hypothesis that the CNS relies on a modular architecture to overcome the complexity of multijoint limb dynamics (Bizzi et al. 2008; Wolpert and Kawato 1998). Muscle synergies and modularity in the control of limb movements have been found in many studies in humans (AjiBOye and Weir 2009; Chvalta et al. 2011; Gentner and Classen 2006; Ivangelo et al. 2007, 2004; Klein Breteler et al. 2007; Krishnamoorthy et al. 2003; Mucell et al. 2010; Torres-Oviedo and Ting 2007, 2010; Weiss and Flanders 2004), monkeys (Holdefer and Miller 2002; Overduin et al. 2008), cats (Krouch et al. 2006; Lemay and Grill 2004; Ting and Macpherson 2005), and frogs (Cheung et al. 2005; d’Avella et al. 2003; Giszter et al. 1993; Hart and Gisztter 2004, 2010; Roh et al. 2011; Saltiel et al. 2001; Tresch et al. 1999). To our knowledge, modularity in adjustments to targeted limb movements has been shown before only in frogs (Cheung et al. 2009; Kargo and Gisztter 2000) and, recently, in humans for a target jump to a single location (Fautrelle et al. 2010). In contrast, our results rely on identifying structural generations underlying intermittent control.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

A. d. and F. L. conception and design of research; A. d. and A. P. performed experiments; A. d. and A. P. analyzed data; A. d. and F. L. interpreted results of experiments; A. d. prepared figures; A. d. drafted manuscript; A. d. and F. L. edited and revised manuscript; A. d., A. P., and F. L. approved final version of manuscript.

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